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Establishment of Mussel Beds: Attachment Behavior and Distribution of Recently Settled Mussels (*Mytilus californianus*)

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Abstract. The distribution and behavior of small *Mytilus californianus* (plantigrades) were studied, and results were interpreted with respect to intertidal community structure and establishment of mussel beds. *Mytilus californianus* plantigrades were found on mussel beds, algae, and bare rock. Highest densities of plantigrades were observed on the red alga *Endocladia muricata.* Field experiments and sample data suggest that algae that grow upon adult mussel shells have no effect on the density of settlers or plantigrades in a patch of mussels. Plantigrades were abundant in established mussel beds throughout the year because settlement is continuous. Laboratory choice experiments indicate *M. californianus* plantigrades do not select particular species for byssal attachment. *Mytilus californianus* beds are established only after a surface has been previously colonized. By settling and surviving upon many different surfaces, *M. californianus* is capable of establishing populations throughout a broad geographic range.

INTRODUCTION

PAST ECOLOGICAL work on the marine mussel *Mytilus californianus* Conrad, 1837, has emphasized population regulation (PAINE, 1966, 1974; ACKERMAN, 1971), competition with other sessile species (PAINE, 1966, 1974; HARGER, 1968, 1970a, b, 1972a, b; SUCHANEK, 1981), infaunal communities (HEWATT, 1935; KANTER, 1977; SUCHANEK, 1979), and the role of mussel beds in community structure (LEVIN & PAINE, 1974; PAINE & LEVIN, 1981). These studies have demonstrated that *M. californianus* is an important species in the intertidal community because of the competitive ability, persistence, and abundance of individuals and populations (mussel beds). However, relatively little work has been done on the attachment preferences and survival patterns of small *M. californianus.* Because adult distribution and abundance patterns are the result of small mussel behavior and survivorship, work on these topics should improve our understanding of intertidal community dynamics and population development of *M. californianus.*

PETRAITIS (1978) compared the distributions of juvenile *Mytilus californianus* and *M. edulis* Linnaeus, 1758, in southern California and concluded that juveniles were more likely to be associated with conspecific adults than adults of the other species. He attributed these distributions to selective settlement (primary settlement) rather than movement of plantigrades (secondary settlement) or juvenile mortality. PAINE (1974) sampled algae, barnacles, and mussel beds in Washington and noted high densities of small mussels (less than 1.5 cm) among "filamentous" algae and the byssal threads of adult mussels.

This study presents data on the behavior and distribution of small, post-settlement *Mytilus californianus.* Specific emphasis is given to the distribution, abundance, and attachment behavior of plantigrades (individuals between 1.0 and 10.0 mm in length). Observed patterns are interpreted with respect to mussel bed establishment and local community structure. Data on primary settlement patterns and pediveliger behavior of *M. californianus* are presented elsewhere (PETERSEN, 1984).

DISTRIBUTION AND DENSITY OF PLANTIGRADES

The major study site was Mussel Reef on Yoakam Point, Oregon (43°20′N; 124°22′W). Mussel Reef is a flat, wavecut platform about 2.0 m above mean lower low water.

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Table 1

Density of *Mytilus californianus* plantigrades on various substrata at Mussel Reef, Oregon. Mean number of plantigrades is given per 100 cm^2 of substratum. Samples were collected in May and June of 1980.

Substratum	Mean	SD	n
Endocladia muricata	260.0	174.5	10
Gigartina papillata	125.0	128.8	5
Cladophora sp.	95.8	137.0	18
Corallina vancouverensis Yendo, 1902	79.3	82.8	6
Rhodomela larix	62.4	37.6	8
Analipus japonicus (Harvey) Wynne, 1971	40.0	33.5	5
Unclassified red alga #1	27.0	29.0	12
Mytilus californianus	21.6	9.1	8
Polysiphonia sp.	10.3	18.3	22
Bare-barnacle	0.0	0.0	9

Table 2

Mean percent cover on shells of *Mytilus californianus* from established mussel beds at Mussel Reef, Oregon. Samples (n = 74) were collected between June 1979 and September 1981.

Substratum	Mean (%)	SD
Bare shell	86.8	7.2
Barnacles	8.8	5.7
Cladophora sp.	1.3	3.6
Polysiphonia sp.	1.1	2.4
Rhodomela larix	0.7	2.9
Endocladia muricata	0.4	1.5
Fucus distichus Linnaeus, 1767	0.3	1.6
Spirorbis borealis Daudin, 1800	0.2	0.5
Anthopleura elegantissima (Brandt, 1835)	0.1	0.3
Corallina vancouverensis	0.1	0.4
Odonthallia floccosa (Esper) Falkenberg, 1901	0.1	0.5
Haliclona sp.	0.1	0.5
Gigartina papillata	<0.1	
Ulva lactuca Linnaeus, 1753	<0.1	
Gelidium sp.	<0.1	
Halichondria sp.	<0.1	
All algae	3.9	7.4

Mussel beds of *Mytilus californianus* and patches of the red alga *Rhodomela larix* (Turner) C. Agardh, 1822, cover most of this sandstone platform (PETERSEN, 1983).

The abundance of plantigrades on several substrata was estimated at Mussel Reef. Pseudo-random points were established by blindly throwing an object onto mussel beds, algal dominated areas, or "bare-barnacle" patches. Bare rock areas usually included many small barnacles (primarily *Balanus glandula* Darwin, 1854, and *Chthamalus dalli* Pilsbry, 1916) so this substratum will be referred to as bare-barnacle. Samples were collected at a pseudo-random point, or as near one of these points as possible. *Mytilus californianus* beds were sampled by collecting all mussels, infauna, and sediment in a 100-cm^2 area. *Rhodomela larix* (25-cm^2 samples) and other substrata (4-cm^2 samples) were sampled by scraping all material in the given area into a plastic bag. Samples were returned to the laboratory and visually or mechanically sorted (PETERSEN, 1983). All mussels less than 10 mm in length were measured to the nearest 0.1 mm with an ocular micrometer; larger mussels were measured with vernier calipers.

Small *Mytilus edulis,* which were occasionally found at the study site (PETERSEN, 1983), and *M. californianus* are morphologically similar, and separation of plantigrades of these species is difficult (SUCHANEK, 1978; personal observation). To develop an identification criterion, *M. edulis* collected in Coos Bay, Oregon, and Spanish Ship Bay, Nova Scotia (supplied by Dr. Gary Newkirk), were compared with *M. californianus* of similar size from Mussel Reef. Individuals greater than 1.0 mm in length differed in the shape of the ventral shell margin immediately posterior to the umbo. The ventral margin of *M. edulis* valves is straight or slightly convex from the umbo to the posterior part of the shell where the margin bends dorsally. However, the ventral shell margin of *M. californianus* plantigrades usually has a small, gentle indentation immediately posterior to the umbo region. Identification of plantigrades was based upon this characteristic of the shell. Mussels less than 1.0 mm in length could not be easily identified to species, so these individuals are referred to as "settlers."

Small mussels were found on all substrata sampled, except the bare-barnacle surface (Table 1). Density was highest on the red alga *Endocladia muricata* (Postels & Ruprecht) J. Agardh, 1847, with 260.0 plantigrades/100 cm^2 of alga. Other algae had plantigrade densities between 125.0/100 cm^2 on *Gigartina papillata* (C. Agardh) J. Agardh, 1846, and 10.3/100 cm^2 on *Polysiphonia* sp. The density of plantigrades in *Mytilus californianus* beds (21.6 plantigrades/100 cm^2) was relatively low compared to other substrata sampled.

The high variability of these data probably indicates a true patchy distribution of plantigrades and not just a sampling problem. All algal and bare-barnacle samples, except *Rhodomela larix,* were 4 cm^2. Because many of the algae sampled occur as small patches, increasing sample size to improve the estimates was not possible. Moreover, the data from *R. larix* samples were also highly variable, although sample size was 25 cm^2 for this species. Increasing the number of samples of a substratum did not seem to improve the estimates; for example, the variation in *Polysiphonia* sp. (n = 22; coefficient of variation = 178%) was greater than for those substrata where fewer samples were taken.

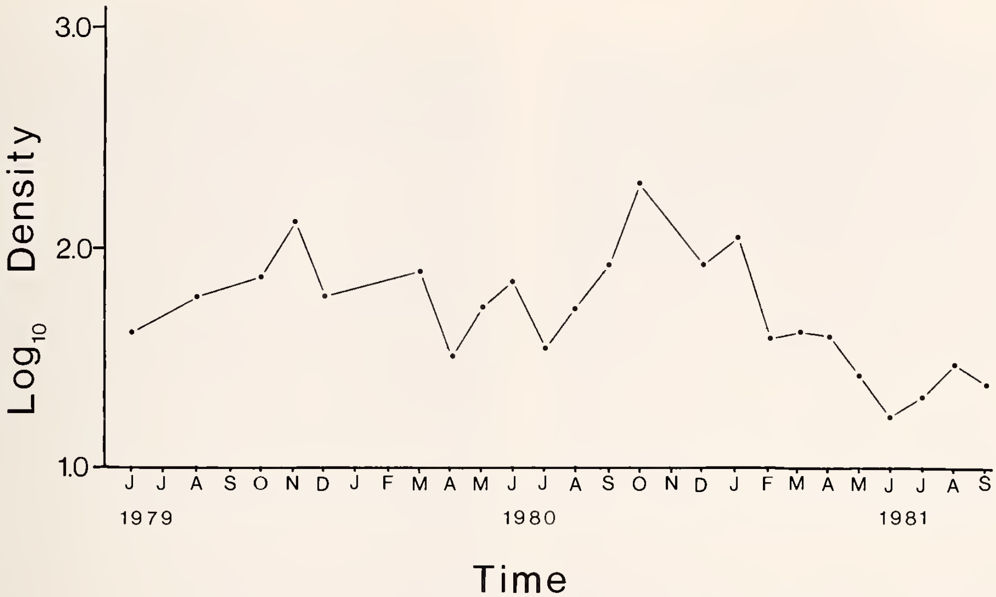

Figure 1

Density of *Mytilus californianus* plantigrades in *M. californianus* beds at Mussel Reef, Oregon. Each point is the mean number of plantigrades per 100 cm^2 of substratum. Most means are the average of four samples.

Plantigrades of *M. californianus* were present in established mussel beds throughout the sampling period (Figure 1). Plantigrade density in *M. californianus* samples followed roughly the same seasonal pattern as settlement density (Petersen, 1984): high numbers of settlers and plantigrades in late summer through fall and lower numbers during other parts of the year. Plantigrade density increased in the fall of 1980, corresponding to heavy larval settlement beginning in June 1980 and peaking in August 1980 (Petersen, 1984; see also Kelley *et al.*, 1982). These summer settlers likely grew into the plantigrade category by fall, causing the increase shown in Figure 1.

ROLE OF ALGAE ON ADULT MUSSEL SHELLS

Several species of algae occur on mussel shells from the central Oregon coast (Table 2). The average cover of algae in all samples was about 4%, whereas the maximum cover was 30% in a sample collected in October 1980. The variation in total algal cover between samples was large because species were patchily distributed over the reef; some areas had a relatively heavy cover of algae and barnacles while in other areas the mussel shells were quite bare. Suchanek (1979) investigated the role of herbivores in mussel beds. When grazers (limpets and littorines, primarily) were removed from a patch of mussels, the percent cover of algae increased dramatically. Many herbivores were found in the samples collected at Mussel Reef, and they may be controlling the overall abundance of algae. These grazers may also be responsible for the patchy distribution of algal species on the mussel beds, if the density of herbivores is uneven across the reef. There were no obvious seasonal patterns in total algal abundance on mussel shells; however, annual species of algae were more abundant at certain times of the year, especially during the spring and summer.

Algae on shells in established mussel beds could affect the recruitment of settlers and plantigrades into the bed in several ways. As a settling larva swims and drifts through the water, it may encounter an algal thallus and begin testing this thallus or the nearby surfaces for their attachment suitability. The larva might attach to the alga itself or it might use the alga as a track to crawl to a more suitable substratum. Algal patches also increase the total exposed surface area of a mussel bed, thus increasing the chance that planktonic larvae will encounter a surface and settle in this area. If the alga has erect thalli, they may function as a net, filtering water moved by waves, tides, and currents.

To test the hypothesis that algae or barnacles on mussels increase larval settlement, or recruitment of plantigrades in the mussel bed, a removal experiment was carried out at Mussel Reef. In March 1980, five 400-cm^2 areas were haphazardly selected within the established mussel bed. In each of the five patches, at least 10% of the exposed shell was initially covered by algae. All of the algae and barnacles were scraped from the mussels in each area with a putty knife and a wire brush (Removal treatment). These five sites were scraped monthly to remove any algae or barnacles that settled on the mussel shells. After 12 months, 100-cm^2 samples were collected from the

Table 3

Density of settlers and *Mytilus californianus* plantigrades in algal removal experiments. Mean number of individuals, with SD, is given per 100 cm^2 of substratum. All data were collected in April 1981. Only those settlers and plantigrades that were attached by byssal threads to adult mussels were included in calculating these means; unattached and algal attached mussels were not included because this is a test of recruitment *into* the mussel matrix. See text for an explanation of controls.

Treatment	Mean	SD	n	F
Settlers				
Removal	6.5	5.0	4	
High % algae control	4.5	6.4	2	0.17 NS
Low % algae control	5.0	2.8	2	
Mytilus californianus plantigrades				
Removal	38.5	21.9	4	
High % algae control	32.5	38.9	2	0.60 NS
Low % algae control	14.0	12.7	2	

NS = Not significant.

Table 4

Results of four-way choice experiments with *Mytilus californianus* plantigrades. E is the expected number of plantigrades attached to a substratum based on the encounter rate for that substratum. O is the observed number of attached plantigrades.

Substratum	Boundary (mm)	O	E	χ^2
	Trial #1			
M. californianus	384	14	16.9	
M. edulis	425	28	18.7	11.2*
Rhodomela larix	427	8	18.8	
Sandstone	331	19	14.6	
	Trial #2			
M. californianus	403	22	17.8	
M. edulis	431	14	19.0	8.5*
Rhodomela larix	384	25	16.9	
Sandstone	323	7	14.3	

* = $P < 0.05$.

center of each 400-cm^2 removal area. One of the five original sites was damaged by winter waves, so only four samples of scraped mussels were collected. Two types of control samples were collected at the same time as the Removal samples: (1) samples that had more than 10% algal cover on the mussel shells (High % Algae Control), and (2) samples that had less than 1% algal cover on the mussels (Low % Algae Control). All samples were returned to the laboratory and processed in the usual fashion.

Data from the algal removal experiments suggest that settlement and plantigrade recruitment were not significantly affected by algae on adult mussel shells (Table 3). Settler densities were similar in all treatments and were not significantly different. Densities of plantigrades ranged from 38.5/100 cm^2 in the Removal treatment to 14.0/100 cm^2 in the Low % Algae Control; there was no statistical difference between treatments. Because variation in both controls and removals was high, a "significant" decrease in the removal series may have been difficult to detect. The relatively high densities of settlers and plantigrades in the Removal treatment, however, suggest there was no effect of removing algae from the adult shells.

Mussel samples collected between June 1980 and January 1981 were also used to test the effects of algal cover. During this period, settlement intensity was fairly constant at Mussel Reef (PETERSEN, 1984). The number of settlers in a sample was not related to the total percent algal cover in that sample ($P > 0.05$, $r^2 = 0.26$, $n = 22$). Also, the number of *Mytilus californianus* plantigrades and the total percent algal cover were unrelated ($P > 0.10$, $r^2 = 0.09$, $n = 22$). This correlative evidence and the removal experiment suggest that the presence of algae on adult mussels does not significantly increase (or decrease) settlement or recruitment into the mussel bed.

PLANTIGRADE SELECTION EXPERIMENTS

The attachment preferences of *Mytilus californianus* plantigrades were investigated in the laboratory with four-way and two-way choice experiments. The four-way choice experiments were run in 30 × 60 cm glass aquaria. *Mytilus californianus* adults, *M. edulis* adults, *Rhodomela larix* thalli, and pieces of bare sandstone were the substrata tested. To make the encounter probabilities of the substrata approximately equal, and to avoid confounding effects of aquarium edges, each substratum was placed in a separate corner of the aquarium, and the inner boundary of a substratum was extended from the midpoint of one side of the aquarium to the midpoint of the adjacent side. This arrangement produced in the aquarium a diamond-shaped arena, the sides of which were the four test substrata. A searching plantigrade in this arena would encounter only the four test substrata and none of the aquarium edges. The expected encounter rate of a substratum was estimated by tracing the boundary of the substratum on paper, measuring the length of this boundary with an opisometer (a map distance-measurement instrument), and calculating what proportion of the total boundary length was attributable to this substratum.

All test substrata and plantigrades were collected from Mussel Reef. Mussels, algae, and sandstone were rinsed, and all animals and algae were removed using a dissecting microscope. Test substrata were placed in an aquarium, water was added, and the setup was left for 24 h before 100 naive *Mytilus californianus* plantigrades were haphaz-

ardly placed in the central arena. Plantigrades were allowed to search and attach for 24 h, after which the substrata were collected and the number of attached plantigrades was determined. During the search period, aquaria were kept in dim, diffuse light and aeration was provided. Two trials of these four-way choice experiments were run.

Table 4 lists the data and analyses of the four-way choice experiments. In the first trial, of those plantigrades that chose a substratum, *Mytilus edulis* adults were preferred (40.6% of all attached individuals). Only eight plantigrades chose *Rhodomela larix* thalli, much less than the 18.8 expected based upon the encounter probabilities. The number of plantigrades attached to sandstone and *M. californianus* were near the expected values. The results of the second trial differed somewhat from the first trial. *Rhodomela larix* was the preferred substratum (36.8% of all attached individuals) and sandstone was least preferred (10.3%). In both experiments, about one-third of the plantigrades tested were found unattached or attached to the glass in the central arena. Although both trials differed significantly from random attachment based upon the calculated encounter probabilities, the different results in the two trials and the high proportion of glass-attached individuals suggest that *M. californianus* plantigrades may not "prefer" any of these substrata over others.

Different results in the four-way experiments could also result from inadequate control of experimental factors; therefore, a second plantigrade attachment experiment was run. *Mytilus edulis, M. californianus,* and *Rhodomela larix* were used as test substrata in two-way choice experiments (Table 5). Each test substratum was distributed in a semicircle around the edge of a 2-L finger bowl, and 30 plantigrades were added to the central area of the bowl. Plantigrades were allowed to search and attach for 12 h before the substrata were removed and examined. Boundaries of the substrata were not measured in these experiments; encounter probabilities of the two test substrata were assumed to be equal. Each experiment was replicated. The distribution of plantigrades was not significantly different from random attachment expectation in any of these experiments. About half (87/180) of the plantigrades used in these experiments were unattached or attached to the glass finger bowl. The conclusions from these experiments are similar to those obtained from the four-way choice experiments: none of the substrata tested appear to be strongly preferred by *M. californianus* plantigrades.

Table 5

Results of two-way choice experiments with *Mytilus californianus* plantigrades. E is the expected number of individuals attached to this substratum based on the assumption of equal encounter probabilities. O is the observed number of attached plantigrades.

Substratum	O	E	χ^2
Mytilus edulis	5	6.0	0.1 NS
Rhodomela larix	7	6.0	
Mytilus edulis	12	8.5	2.1 NS
Rhodomela larix	5	8.5	
Mytilus californianus	9	8.5	0.0 NS
Rhodomela larix	8	8.5	
Mytilus californianus	5	9.5	3.4 NS
Rhodomela larix	14	9.5	
Mytilus californianus	7	6.5	0.0 NS
Mytilus edulis	6	6.5	
Mytilus californianus	4	7.5	2.4 NS
Mytilus edulis	11	7.5	

NS = Not significant.

DISCUSSION

Some marine mussels, particularly *Mytilus edulis* studied in Europe, go through two attachment phases called primary settlement and secondary settlement (BAYNE, 1964, 1976; SEED, 1969). As larvae settle from the plankton, they test various substrata and select a primary attachment site (primary settlement). Primary settlement is often on a filamentous alga (BAYNE, 1964; PAINE, 1974; PETERSEN, 1984). Secondary settlement is movement and reattachment of small mussels, usually when individuals are greater than 1.0 mm (BAYNE, 1964). Movement is often onto an established mussel bed (BAYNE, 1964). BAYNE (1964) suggested this behavior reduces competition between juvenile and adult *M. edulis*. Whether *M. edulis* has similar behavior on American shores is not known (SUCHANEK, 1978).

Studies on settlement and distribution of small *Mytilus californianus,* including this paper, have not demonstrated secondary settlement behavior in this species (PAINE, 1974; PETRAITIS, 1978; SUCHANEK, 1981; PETERSEN,1983). In laboratory choice experiments, *M. californianus* larvae preferred adult clumps of *M. edulis* (PETERSEN, 1984). In field samples, *M. californianus* has been found on a variety of substrata, particularly filamentous algae and byssal threads of adult mussels (PAINE, 1974; SUCHANEK, 1979; PETERSEN, 1984). These results suggest that *M. californianus* settles broadly if its preferred substratum, *M. edulis,* is unavailable. In areas where *M. edulis* patches are common, *M. californianus* may select these patches over other available substrata; however, more work needs to be done on settlement preferences in the field.

Mytilus californianus settlers survive to the plantigrade stage on a variety of substrata. Only bare rock and barnacle-covered rock were barren of *M. californianus* plantigrades, although densities were fairly low in some patches of algae, such as *Polysiphonia* sp. Some surface cover is apparently necessary for larval settlement and plantigrade attachment.

Algal and mussel patches undoubtedly have many crevices and holes where plantigrades can attach and receive some protection from wave battering and predators. Plan-

tigrades are often found in the axils of thalli, in the crevice between adult mussel valves, and in cracks in rocks. Such microhabitats offer physical protection, and plantigrades may also be more secure when their byssal threads are attached to many different surfaces, rather than just one flat surface.

Differential predation rates might also explain the distribution of plantigrades. Many animals, including seastars, gastropods, crabs, and birds, are known to prey upon mussels (*e.g.,* NORTON-GRIFFITHS, 1967; HARGER, 1972b; PAINE, 1974; SEED, 1976).

Some shore birds—*e.g.,* Surf Birds, *Aphiza virgata* (Gmelin), and Black Turnstones, *Arenaria melanocephala* (Vigors)—prey upon small mussels along the central Oregon coast, eating both *Mytilus californianus* and *M. edulis* (Chris Marsh, personal communication). Searching by these birds may be more efficient on bare and barnacle-covered rock surfaces, leading to complete removal of all recent settlers and plantigrades. Predation in algal patches could be less efficient because some plantigrades might be overlooked by the birds and thus survive. *Nucella emarginata* (Deshayes, 1839) is an important gastropod predator on large mussels, particularly *M. edulis* (PARIS, 1960; DAYTON, 1971; HARGER, 1972b; SUCHANEK, 1978), but no studies have concentrated on the effects of this snail on plantigrades. Many small mussel shells with gastropod bore holes were found in the samples of algae and mussels collected at Mussel Reef. Plantigrades are undoubtedly eaten by these gastropods although the intensity of predation in different patches is unknown. *Nucella* exclosure experiments were attempted but were unsuccessful because of severe weather and vandalism. The role of other predators in controlling the abundance and distribution of small *M. californianus* has not been investigated although there has been speculation on this subject (SUCHANEK, 1979).

The primary settlement behavior (PETERSEN, 1984) and plantigrade survival patterns of *Mytilus californianus* may help to explain how mussel beds are established and persist through a broad geographic range. *Mytilus californianus* forms extensive beds on exposed rocky shores from Mexico to British Columbia (SOOT-RYEN, 1955; SUCHANEK, 1981). Disturbances occur periodically within this range, removing patches of established mussel beds (DAYTON, 1971; personal observation). Succession within cleared areas culminates in new *M. californianus* beds which persist until another disturbance occurs. In Washington, patches are filled by algae, *M. edulis,* and finally *M. californianus,* which settles among *M. edulis* patches and eventually excludes this competitively inferior mussel (PAINE, 1974; PAINE & LEVIN, 1981). However, because *M. edulis* is not very common on central Oregon shores (PETERSEN, 1983), and perhaps in other local areas, the recovery pattern may be somewhat different.

If *Mytilus edulis* patches were required for *M. californianus* colonization, the sequence leading to mussel bed recovery would be incomplete in geographic areas where *M. edulis* is sparse. However, *M. californianus* larvae begin to settle once a disturbed area has been colonized by algae. Continual reproduction and broad larval preferences ensure that some settlement will occur on various algae. Pediveligers attach to many surfaces (PETERSEN, 1984) and plantigrades survive on most substrata, particularly those with small holes and crevices. This general attachment behavior of *M. californianus* pediveligers and their survival on diverse substrata assure a broad distribution of growing mussels in the disturbed area. As plantigrades grow, they gradually fill the original disturbed patch, attach to the rock, and exclude other species (PAINE & LEVIN, 1981). The dynamics of patch recovery may be altered because the survivorship rate of *M. californianus* is probably different in algal patches than in *M. edulis* patches, but the mechanism for mussel bed recovery remains intact.

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